A NEW OWLET-NIGHTJAR FROM THE EARLY TO MID-MIOCENE OF EASTERN NEW SOUTH WALES

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Abstract

A new owlet-nightjar (Family: Aegothelidae), *Quipollornis koniberi* gen. et sp. nov., has been recognized from Miocene lacustrine sediments in eastern New South Wales. It thus establishes the occurrence of the aegothelids in Australia during the Miocene. The new form shows distinct and numerous differences from the other two genera in this family, the living *Aegotheles* from Australia, New Guinea, and the South-west Pacific and its closely related New Zealand counterpart, *Megaegotheles*, now extinct.

Introduction

During the past 50 years diatomite deposits representing mid-Tertiary freshwater lakes in eastern Australia have yielded a number of well-preserved leaves and fish. Among these collections is a single, unique skeleton of a small bird closely related to the living Owlet-nightjars (*Aegotheles*), nocturnal birds endemic to, but with wide dispersion in, Australia, New Guinea, and the South-west Pacific. The Miocene fossil, *Quipollornis koniberi* gen. et sp. nov., is the oldest record of the family Aegothelidae, which is represented by only one other genus, the extinct *Megaegotheles* (Scarlett, 1968; Rich and Scarlett, 1977) from the Quaternary of New Zealand. This paper describes the new form and compares it with all other caprimulgiform families.

In this study the following forms were available to us for comparison: *Steatornis caripensis* (1), *Nyctibius griseus* (3), *Podargus strigoides* (20), *Aegotheles cristatus* (9), *Eurostopodus guttatus* (5), *E. mysticalis* (3), and *Chordeiles minor* (1).

Systematics

Class: Aves

Order: Caprimulgiformes (Ridgway) Brodkorb, 1971

Family: Aegothelidae (Bonaparte)

Comment: Placement of *Quipollornis koniberi* gen. et sp. nov. in the Aegothelidae is based primarily on its broad skull with slender-boned lower and upper jaws and rounded, inflated braincase; its highly curved internal margin of the coracoidal head; and its short but broad cervical vertebrae. This combination of characters appears to be unique to the Owlet-nightjars within the Caprimulgiformes.

Quipollornis gen. nov.

Type Species: Quipollornis koniberi gen. et sp. nov.

Age and Distribution: Early to Middle Miocene, eastern New South Wales, Australia.

Etymology: Quipolly (Aboriginal), a waterhole containing fish; *ornis* (Greek), Bird. Referring to the occurrence of *Quipollornis* in lacustrine sediments containing mainly fish.

Diagnosis: Differs from *Aegotheles* in that the jugals are broader and stouter bones, and the maxillaries do not expand as much mediolaterally towards their posterior termination. Differs from both *Aegotheles* and *Megaegotheles* in that the head of coracoid is not as inflated dorsally and is decidedly more elongate between the coraco-humeral surface and procoracoid; the scapula appears to lack a marked flexure near the posterior end as well as expansion of the posterior end present in *Megaegotheles*; the breadth of the scapula just anterior to the glenoid facet is somewhat greater than in *Aegotheles*, similar to that area in *Megaegotheles*; the deltoid crest is intermediate in its dorso-lateral protrusion between *Megaegotheles* and *Aegotheles*; the metacarpal I process is lower and broader, and metacarpal III markedly more robust. Differs from *Megaegotheles* in that the shaft (viewed ventro-laterally) is not as highly curved.

Ratios (see Table 1). The humerus about twice the length of femur unlike that of

TABLE I: Meesurements (in mm.) of Skull, Shoulder Girdle, and Limbs of Quipollornis koniberi, n. gen. et n. sp. and Other Ceprimulgiforms.

Specimens Measurements	Podargus strigoides	Eurostopodus mystacalis	Eurostopodus guttetus	Aagothales cristatus	Staatornis ceripansis	Nyctibius griseus	Quipollornis koniberi AMF48404-5 rt.	Quipollornis koniberi AMF48404-5 lf.	Megaagothales novaezaelendiee
Skull									
Width	49.3-55.4 (6)	30.0	24.8 (l)	22.8-23.6	34.4	43.1-47.2		30.8	26.0-27.0
Length	81.5-88.7	52.6	⩾44.0-48.4 [4]	35.4-38.4	60.1	66.8-65.1		40.8	-
Width/Length	0.58-0.68	0.57	0.51	0.61-0.65	0.57	0.73-0.76		0.75	
n	7 (6)	1	2(l)	6	1	3		1	2
Scapula									
Length	38.2-43.7	32.8-34.4	26.4-27.9	19.0-23.4	46.2	34.9-39.2	⩽21.2	⩾23.3	25.8
Maximum width,heed	9.6- 11.3	5.3- 6.7	4.8- 5.6	4.2- 5.1	8.8	7.4- 7.5	5.3	5.6	-
n	8	3	3	8	1	3	1		1
Coracoid									
Length of head [1]	8.0- 8.5	6.9- 7.7	6.8	4.2- 4.6	6.4	7.0- 9.2	4.8		4.7
Width across head [2]	4.5- 5.5	3.9- 5.7	3.2	1.3- 2.0	7.4	3.6- 5.3(2)	2.8		2.1
n	3	2	1	7	1	3(2)	1		1
Humerus									
Length	76.0 - 81.7 (6)	53.2-54.7	43.5-47.2	26.6-28.4	69.2	59.8-67.3	@35.0 [4]	34.9	28.3-36.3(20)
Maximum width proximal end [3]	17.4 - 21.6	12.9- 18.1	12.9- 14.6	8.1 - 9.1	20.9	16.8-20.2	@10.0	@11.2	6.8- 8.0(20)
Maximum width distal end	13.7- 14.8	8.8- 10.1(6)	7.8- 8.4	5.6- 6.2	14.3	10.7- 12.9	-	@ 7.1	5.3- 7.0
n	7 (6)	3	3	7	1	3	1		22(20)
Ulna									
Length	81.7- 86.8	67.4-67.8	57.4-63.0	32.8-34.9	103.2	63.4-72.0	-	est. 44.5 [5]	32.5-39.3
Maximum diameter, axternal condyla	6.9- 7.4	5.0- 5.8	4.0- 4.5	2.7- 3.1	7.0	5.8- 6.9	-	@ 4.4	3.3- 3.4(3)
n	8	3	3	8	1	3	1		4(3)
Carpometacarpus									
Length from head to distal end of inter-metacarpal space	32.0-36.6	30.6-31.3	27.7-29.1	15.2- 16.7	37.6	24.8-31.1	-	19.8	16.7
Minimum width of metacarpal II	2.0- 2.5	2.2- 2.3	1.7- 1.8	0.9- 1.2	2.5	2.4- 3.1	-	2.9	1.7
Length of intermeta-carpal space	19.8-24.1	21.2-21.8	19.8-20.6	9.4- 11.2	22.7	14.8- 18.8	-	11.6-	11.4
n	8	3	3	8	1	3	1		1
Carpal Phalanx I									
Length	8.6- 12.2	10.6	7.9	5.6	13.8	10.1	-	5.6	-
n	5	1	1	1	1	1	1		-
Femur									
Length	40.2-43.1	28.5-29.2	24.2-26.1	20.5-22.0	35.1	27.6	⩾17.5		23.0-32.0
n	8	3	3	8	1	2	1		7
Tibiotarsus									
Depth, proximal end	7.8- 8.8	4.5- 5.4	3.7- 4.1	3.4- 4.3	7.4	5.0- 6.3	4.6	5.7	6.4- 6.5(2)
Length	62.4- 71.2	38.6- 39.4	34.0-38.4	35.4- 38.0	43.5	35.6-42.1	⩾22.1		50.0- 66.0+
n	8	3	3	7(6)	1	3	1		12(2)
Ratios									
Humeral Length / Ulnar Length	0.84- 0.93	0.78- 0.81	0.740.76	0.78- 0.81	0.67	0.93-0.96		0.78	0.87-0.92 [6]
Humeral Length / Femoral Length	1.76- 1.94	1.82- 1.91	1.80-1.84	1.26- 1.32	1.97	2.17-2.22	2.0	-	1.13 - 1.23
Humeral Length / Skull Width	0.92- 0.97	1.04	0.930.99	0.72-0.76	2.01	1.02- 1.03	1.14	1.13	1.09- 1.34
Humeral Length / Proximal Width Humerus	3.70- 4.12	3.01 -3.13	3.17- 3.37	2.92-3.24	3.31	3.33-3.65	3.5	3.12	4.03- 4.16
Humeral Length / Distal Width Humerus	5.54- 5.83	5.16- 5.43	5.36-6.05	4.39-4.82	4.84	5.22-5.74		4.92	5.19- 5.34

FOOT NOTES:

1. Length of coracoid from dorsalmost part of head to ventralmost part of curve betwean procoracoid and brachial tuberosity.
2. Width from distalmost extension of curve to external margin of shaft.
3. Width across heed to maximum expansion of deltoid crest.
4. @, approximately, ⩾⩽, slightly greater or slightly less than.
5. Measurement mede by utilizing complete humerus on counterpart to project where proximal end of ulna would occur on other slab.
6. Because none of the Megaegotheles except one where definitely associated, ratios have been computed by considering minimum measures togethar and maximum meesures likewise.

Megaegotheles and *Aegotheles* where humerus and femur are nearly subequal; the humerus is slightly longer than the width of the skull as in *Megaegotheles*, but unlike *Aegotheles* in which the skull is broader than the length of humerus; humerus broader distally with respect to its length than that in *Megaegotheles*, although quite similar to that of *Aegotheles*.

Comparisons: Skull. The occipital region of cranium is rounded posteriorly (convex posteriorly) unlike the flattened posterior edge in *Eurostopodus* and *Caprimulgus*, the slightly concave edge in *Nyctibius*, and the slightly convex edge in *Podargus* and *Steatornis*; the dorsal surface of cranium lacks the well-developed, paired temporal fossae that occur in *Podargus* and *Steatornis*. Such fossae are only slightly developed in *Aegotheles*, are situated much more ventrally, and thus are not evident in dorsal view; the premaxillaries, maxillaries, and nasals are very slender as in *Aegotheles*, but unlike the fully fused elements in *Podargus* and *Steatornis* that form a completely enclosed and continuous upper jaw or the much exanded premaxillae and maxillae in *Eurostopodus* or the elongate and very slender premaxillae that merge into a broad, nearly continuous palate (except for a slender slit along the midline) in *Nyctibius*; the external nasal opening extends further forward than in all genera examined except *Aegotheles*; the upper jaws, viewed dorsally, rapidly expand posteriorly, closely resembling *Aegotheles*, but unlike the gradual expansion that occurs in *Eurostopodus*, *Caprimulgus*, *Chordeiles*, and *Steatornis* resulting in a narrow V-shaped skull or bill or in *Podargus* and *Nyctibius* that have a slightly broader V-shape. The skull is very broad proportionally, decidedly more so than in *Eurostopodus* and *Steatornis*, but closer to that of *Podargus*, *Aegotheles*, and *Nyctibius*. A delicate, short anterior nail is formed as in *Aegotheles*.

Vertebrae (see Table 2). All cervicals preserved are broad with respect to length. In what are probably cervicals 4 and 7 the breadth across anterior zygopophyses is greater than vertebral length; in *Podargus*, *Eurostopodus*, *Steatornis*, and *Nyctibius*, anterior width never exceeds length on any of cervicals 3-6; in *Chordeiles*, width doesn't exceed length in cervicals 5-7; in *Aegotheles*, width and length are nearly the same in cervicals 3-7, with a resulting shorter neck than in most caprimulgiforms in this form and in *Quipollornis*.

Scapula. The breadth of the scapula just anterior to the glenoid facet somewhat narrowed, intermediate between the narrow scapula of *Aegotheles* and the somewhat broader one of *Eurostopodus* and *Chordeiles* but decidedly narrower than that in *Podargus*, *Nyctibius*, and *Steatornis*; the lateral margin of the shaft is not highly curved as in *Steatornis* and *Nyctibius*. (The entire scapula is not preserved, but enough remains for the beginning of expansion to be evident if present; the left scapula, in fact, appears to be nearly complete.)

Coracoid. The medial margin of head between the brachial tuberosity and the procoracoid is highly curved with procoracoid extending so far dorsally that it leaves only a small gap between it and brachial tubcrosity as in *Aegotheles*, and unlike the less highly curved margins and broader gaps characteristic of *Podargus*, *Eurostopodus*, *Chordeiles*, *Steatornis*, and *Nyctibius*.

Humerus. The bone is relatively more robust than in other caprimulgiforms; angle formed between the shaft and proximal margin of bicipital crest is small obtuse angle as in *Steatornis*, *Nyctibius*, *Chordeiles*, and *Aegotheles*, but differs from *Podargus* and *Eurostopodus*; deltoid crest is not as prominent dorsally but is lower and gently rounded throughout, unlike that in *Aegotheles*, *Eurostopodus*, and *Chordeiles*; deltoid crest is also not as broadly expanded from the shaft as in *Steatornis*.

Radius-ulna. The distal end of radius is much more closely appressed to distal end of ulna than in *Steatornis*, *Nyctibius*, and *Chordeiles*.

Carpometacarpus. Differs from other caprimulgiforms in that the process of metacarpal I appears to be lower and more rounded; angle formed between proximal margin of carpal trochlea (viewed externo-dorsally) and long axis of shaft is more acute; the bone is shorter and much more robust, and metacarpal III is

TABLE 2: Vertebral Measurements of Quipollornis koniberi, n. gen. et n. sp., and Other Caprimulgiforms (in millimeters).

Specimen Measurements	Podergus strigoides NMV 8 10178	Eurostopodus guttatus NMV 10647	Aegotheles cristatus NMV 11033	Steetornis caripensis UCMVZ 141741	Nyctibius griseus UCMVZ 126575	Quipollornis koinberi AMF 49404-5
Cervical 4						
Anterior width	8.3	5.0	5.0	7.2	7.1	
Posterior width	7.4	5.6	@ 3.7	7.5	6.5	8.0
Leest width	5.0	5.6	2.0	4.2	6.3	-
Left length	11.2	6.2	4.7	9.8	7.5	6.7
Right length	11.2	6.2	4.7	9.6	7.6	
Cervical 7						
Anterior width	11.4	6.2	6.1	10.7	9.5	7.4
Posterior width	9.1	4.6	3.6	6.6	6.2	7.4
Leest width	3.9	2.4	2.1	3.8	3.0	-
Left length	10.5	7.6	4.2	9.8	7.4	5.4
Right length	9.8	7.7	4.3	9.6	8.7	5.4

@ = approximately

relatively stouter with respect to metacarpal II. The ventral border is slightly more bowed than we observed in other caprimulgiforms.

Femur. When viewed laterally, the bone is parallel-sided over much of its length rather like all caprimugliforms except *Steatornis* where shaft margins diverge towards either end of bone from central part of shaft.

Tibiotarsus. See comment, below.

Feather Impressions. Lateral to the region of the pectoral girdle and the cervical vertebrae are the impressions of contour feathers. These, however, do not show normal feather shape or structure. They preserve the appearance that can be achieved by wetting soft aegothelid contour feathers so that the barbs in each one cling to the rachis, and the feather then takes on a narrow, slender structure. This process is, of course, consistent with the mode of preservation of the fossil specimen. Viewed in this light, the feathers would appear to be typical of, but rather longer than, the soft contour feathers of the living *Aegotheles*. Because of the lack of detail on the fossil feathers, however, it would be fruitless to carry the comparison further, or to claim that the feathers are closer in morphology to *Aegotheles* than to a number of other birds.

Comment: Because only a dorsal view of the specimen has been preserved, ventral elements such as the sternum and more lateral ribs cannot be discerned. Dorsal elements, however, such as vertebrae are readily visible, at least in part.

Vertebrae preserved in *Quipollornis* exhibit a distinct constriction at the fore-aft midline. If cervicals 3 and 4 are represented in this series, their morphology differs from that in *Eurostopodus*, *Steatornis*, and *Nyctibius*, where no such constriction occurs, but is similar to that in *Aegotheles* and *Podargus*.

Besides the vertebrae, many of the elements discussed in the diagnosis are obscured so that interpretation is often difficult and tentative. The posterior ends of the scapulae are missing, and thus whether the scapula was curved near the end or not is unknown. Likewise, the ventral halves of the coracoids are not visible. The humerii are difficult to interpret because one cannot be certain of their precise orientation, and slight differences in perspective can produce apparent radical differences in shape of the deltoid crest and in the prominence of the external tuberosity along the margin between the head of the humerus and the deltoid crest. The proximal end of the carpometacarpus is somewhat obscured by the distal end of the ulna; similarly, the femora and proximal parts of the tibiotarsii are either lacking or obscured with bone hash to the extent that few qualitative statements can be made concerning those bones.

Quipollornis koniberi sp. nov.

(Plate 8, fig. A-B)

Holotype: Australian Museum (AM) No. F49404 and F49405, partial flattened skeleton or its impression in diatomite, including part and counterpart blocks that partly overlap

Representation on these blocks comprises a complete, but partially obliterated skull, 4-6 cervical vertebrae that may represent cervicals 4-8 or 10, scapulae, a partial right and possibly part of the head of the left coracoid, humerii, partial radii and ulnae, the left carpometacarpus and alulu, partial right and left femora and tibiotarsii, possibly the anterior part of the synsacrum, as well as a number of feather impressions that suggest feathers were wet when bird preserved, with barbs closely adhering to the rachis.

Type Locality and Age: Diatomaceous earth deposit at Chalk Mountain, Bugaldi, near Coonabarabran, Warrumbungle Mountains, eastern New South Wales; Early to Middle Miocene.

Measurements: See Tables 1 and 2.

Etymology: Koniberi (Aboriginal), name of tribe that once inhabited the geographic area from which *Quipollornis* was recovered.

Diagnosis: Same as for genus.

Stratigraphic Position

Diatomite deposits from the Coonabarabran area in New South Wales have long been known to produce fossil leaves and fish (Kenny, 1924), the fish being studied some time ago (Hills, 1946) and found to be close to, if not conspecific with, the Murray Cod (*Maccullochella macquariensis*). The leaves, placed in the genus *Cinnamomum* (David, 1950), suggest the presence nearby of rainforest, but its extent is unknown.

Conveniently, the Warrumbungle volcanics also occur in this area and are known to overlie the diatomite deposits producing the fish and aegothelid (Dulhunty and McDougall, 1966; David, 1950). These volcanics have been dated using the potassium-argon technique and range in age from 13·5 to 17 million years B. P. (Dulhunty and McDougall, 1966; Wellman and McDougall, 1974). No vulcanism is known in eastern New South Wales younger than 10 million years ago, so a minimum date of mid-Miocene can be assigned to the Chalk Mountain deposits and their included fossils.

Discussion and Conclusions

Upon first glance, the fossil bird skeleton preserved in the two diatomite blocks from Bugaldi appears to retain exquisite detail, but upon close perusal, it becomes evident that the only parts distinct enough for taxonomic use are the skull, the cervical vertebrae, part of the shoulder girdle and forelimb. Other bones in the skeleton do not contradict the assignment of this form to the Aegothelidae, but, likewise, do not provide any qualitative characters that can be used to distinguish *Quipollornis* from other members of the family.

Within the Aegothelidae, *Aegotheles* and *Megaegotheles* are very similar to one another (Scarlett, 1968; Rich and Scarlett, 1977) and together form a subunit that is distinct from *Quipollornis*. The main differences between the two groups are in relative size of the jugals, shape of the head of the coracoid, shape of the scapular shaft, shape of the metacarpal I process on the carpometacarpus, and the relative lengths of the humerus and femur. Because of the difference, the forelimb seems to have been decidedly more elongate in *Quipollornis* than in other aegothelids (see Table 1), characteristic of the non-aegothelid caprimulgiforms, and thus the marked emphasis placed on hind limbs in the Owlet-nightjar group had not as yet begun to develop significantly.

Despite such differences from the Pleistocene and living aegothelids, *Quipollornis* clearly belongs to this family, and establishes that many of the cranial specializations of the family had already developed some 20 million years ago. However, as mentioned above, emphasis on the hind limb at the expense of the wing had not begun, suggesting a primitive condition for *Quipollornis* within the aegothelids. Such lack of emphasis on the hind limb further suggests that *Quipollornis* was an aerial 'insectivore' like most caprimulgiforms rather than primarily a terrestrial forager, as are the Owlet-nightjars.

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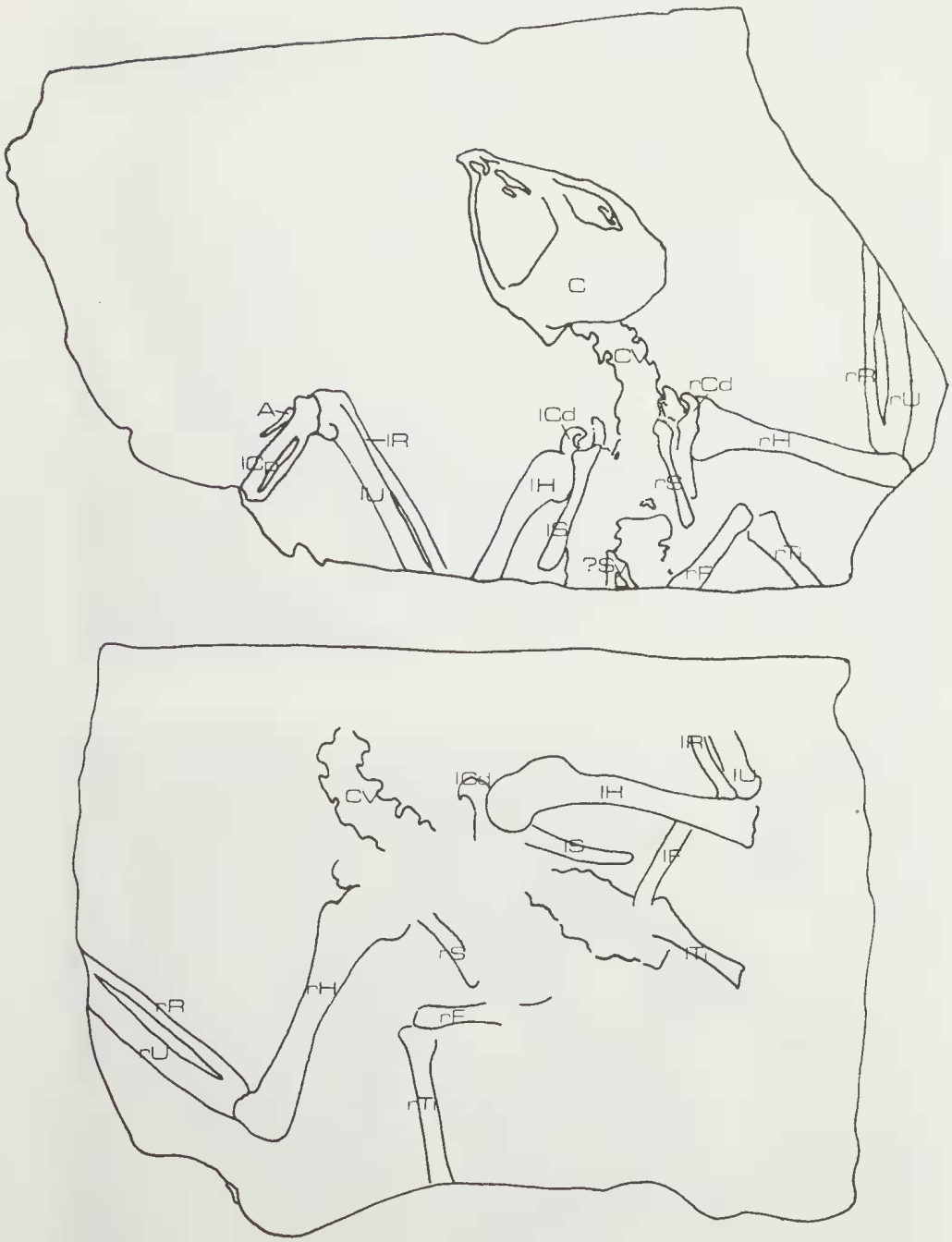

Explanation of Plate 8

Quipollornis koniberi gen. et sp. nov. Abbreviations include: A, alula; C, cranium; CV, cervical vertebrae; lCd, left coracoid; lCp, left carpometacarpus; lF, left femur; lH, left humerus; lR, left radius; lS, left scapula; lTi, left tibiotarsus; lU, left ulna; rCd, right coracoid; rF, right femur; rH, right humerus; rR, right radius; rS, right scapula; rTi, right tibiotarsus; rU, right ulna; ?Sy, possible synsacrum; Fig. A, AM F49404, block containing skull opposite counterpart; Fig. B, AM F49405, counterpart block, see scale for size. Fig. A printed at slightly smaller scale than Fig. B.